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AN EXPERIMENTAL STUDY OF HABITAT SELECTION BY PRAIRIE AND FOREST RACES OF THE DEERMOUSE, PEROMYSCUS MANICULATUS

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INTRODUCTION

ANIMALS are not distributed at random over the surface of the earth. Each species is restricted in the extent of its distribution by the limits of its physiological tolerances to the physical and biological factors of its environment. A species, however, rarely occurs everywhere within the geographical area fixed by these tolerances. Every species is more or less restricted to certain habitats within its geographical range, though it may not live in all those habitats that appear to be similar. Each kind of animal evidently prefers a certain type of habitat to other types and consequently must have some means of selecting the one preferred.

The purpose of the investigation herein reported was to study and to measure some of the factors governing the selection of habitats by small mammals. The experimental animals, Peromyscus maniculatus gracilis, the forest deermouse, and P. m. bairdi, the prairie deermouse, were chosen for study because of their rather definite habitat restrictions in nature and because of their availability in the laboratory. The investigation was carried out under laboratory conditions in order to control more precisely the many factors in the animals' environments. The approach was psychological in that 2 different habitats were presented to the mice for selection in each experiment.

Acknowledgments

This study was carried out under the direction of Professor Lee R. Dice to whom I wish to express my appreciation. Dr. C. C. Craig and other members of the Statistical Research Laboratory, University of Michigan, guided me in the statistical analysis of the data, and Dr. Craig adapted the theory of estimation of missing values to the particular analysis presented herein. Advice and suggestions in statistical matters were also given by Dr. C. W. Cotterman. Philip J. Clark made tests on mice during my absence. The Laboratory of Vertebrate Biology, University of Michigan, provided the reaction room and supported the study with materials, equipment, and experimental animals.

METHODS AND MATERIALS

Description of the Reaction Room

The experiments were conducted in the reaction room of the Laboratory of Vertebrate Biology. A sheet-metal partition 24 inches high divided this room into 2 compartments, each 9 by 10 1/2 feet. The room was nearly light tight and was painted a flat black on the inside. Air ducts leading into the room were equipped with light traps. Ventilation was provided by a fan which blew air into one end of the room through a duct near the ceiling. The air passed out through a similar duct at the other end of the room. The door was near one end of the room.

The lights were connected with a control panel which was outside the room. An electric light socket on the ceiling over the middle of each compartment was equipped to provide various low intensities of light by use of paper disks fastened below the bulb (Dice, 1945:386). Each central fixture in the 2 compartments was surrounded by a cluster of 3 light sockets. These 6 lights were wired through a time clock on the control panel. With this equipment alternating periods of bright light and of dim light or darkness could be produced in the room.

Artificial Habitats

In order to place the study of habitat selection on an experimental basis, standardized and to some extent simplified objects were provided to simulate the vegetational forms present in natural habitats.

The principal features of the artificial forest or tree-trunk habitat (Pl. I, Fig. 1) comprised 9 sections of tree trunks with bark adhering. These trunks varied in height from 20 to 48 inches and in diameter from 2 to 10 inches.

Artificial grass was made from stiff Manila folders. Each half of a folder (9 by 12 inches) was cut into strips about 3/8 inch wide for almost its whole length. The uncut part of each half folder, with the cut strips attached, was then rolled and fastened with Scotch tape, so that its base formed a short cylinder. The pointed end of a nail, driven completely through a lath, formed a support for the cylinder which was inserted over the nail. When the cylinder was placed in an upright position on the lath, the free ends of the cut strips drooped over to resemble a tuft of grass. These tufts of artificial grass were placed at intervals along the lath, and the laths were placed in the compartment about 1 foot apart in parallel formation. One open spot of a few square feet was left near the center of the compartment, as well as a path along 1 side. Otherwise, the tufts of artificial grass covered the floor of a compartment to provide the artificial-grass habitat (Pl. I, Fig. 2).

An intermediate type of habitat resembling a stylized form of shrubbery was provided by the "jungles" developed and described by Dice (1947:8). These were made of strips of wood, as shown in Plate II, Figure 1. The jungles were spaced to cover most of the floor of a compartment, leaving aisles by which the compartment could be entered.

White silica sand covered the floors of the compartments in all the experiments. Besides providing for the mice a more natural floor than the cement, it recorded their tracks and thus gave information about their activity.

Methods of Measuring Habitat Selection

Habitat selection by the mice of the 2 subspecies of Peromyscus tested in the experiments was measured by (1) the amount of food eaten, (2) the amount of water consumed, (3) the number of revolutions made in the activity wheel, and (4) the total time spent in each of the 2 artificial habitats. A food dish, a water tube, a nest box, and an activity wheel were placed in corresponding positions in each compartment.

A definite number of sunflower seeds was counted every day into each food dish. The mice sometimes removed many of these seeds and stored them under the sand. The number of seeds eaten was ascertained by counting the number of whole seeds in the dish, adding the number eaten as estimated from the empty shells, and then, if the original number was not accounted for, searching for those that were stored. Looking for the stored seeds was not entirely a random process since many mice preferred certain spots for storing, and buried seeds could often be detected by the disturbed and heaped-up sand. The error of this estimation for seeds eaten seldom exceeded 2 or 3 per cent. If, according to this estimate, too many seeds seemed to be missing, the data were discarded. By this method one could also ascertain if seeds were carried from one compartment to the other. Actual evidence for this was rarely obtained.

Water tubes were made by sealing the open ends of ordinary culture tubes to openings of about 3 mm. in diameter. Each tube was held by a wire clamp and was hung on a rack with the open end down (Pl. II, Fig. 2). The amount of water consumed by each mouse each day could be determined by refilling the tube from a burette graduated to 0.2 ml. As thus measured, the amount of water consumed included evaporation from the tubes, which averaged about 0.2 ml. per day.

The activity wheels (Pl. I, Fig. 2) were adapted by Sumner (1932:91) from a design by Richter and Wang (1926). Each was constructed of a plywood disk about 9 inches in diameter around which was fastened a piece of hardware cloth 4 3/4 inches wide. The wheel, which weighed approximately 350 gm., was mounted on a ball-bearing axle fastened to a standard and was equipped with a counter that recorded the number of revolutions. An opening through the standard led to the inside of the wheel. The number of revolutions made by the mouse was recorded each day, and the counter was then reset at zero.

Nest boxes were made from aluminum saucepans 6 inches in diameter and 2 1/2 inches deep (Dice, 1929:119). An entrance was cut from the side of a saucepan which was inverted over a piece of masonite. The box was then provided with a small amount of cotton for nesting material.

Apparatus for Recording Time Spent in Each Compartment

To allow the mice access to both compartments, a runway was built over the partition which divided the room. The base of the middle section of the runway consisted of a board that rested horizontally across the partition. At each end it was connected with the floor by a sloping board about 33 inches long. The sloping boards were covered with fine wire screen to make climbing easier for the mice.

The horizontal part of the runway was enclosed by sheet-metal sides and a transparent celluloid top (Pl. I, Fig. 1). The latter was intended to prevent the runway from becoming a darkened retreat attractive to the mice. Each end of the enclosed part was surrounded by shields placed perpendicular to the entrance to prevent the mice from jumping to the partition of the room from the sloping part of the runway.

The enclosed middle section of the runway contained the electrical contact mechanism (Fig. 1) which reported the movements of the mice in the runway to the recording apparatus outside the room.

To travel from one compartment to the other a mouse was required to pass through 2 swinging screen doors which hung down into the passageway. When a door was pushed open, the arm of the door made a contact with a pliant brass strip and closed an electrical circuit to the recording apparatus. This circuit energized an electromagnet which attracted 1 end of the horizontal arm of the recording apparatus built on the plan of a kymograph penholder. The contact made by the doors may have been momentary, and the attracting force of the electromagnet may thus have been of short duration, but a locking device prevented the arm of the recording apparatus from bouncing.

When the mouse again passed through the runway apparatus on its way to the other compartment, the door which last made contact was pushed open toward the center of the enclosed runway, and the electric circuit was not closed except perhaps momentarily as the door swung back into place. No change in record occurred, however, because the horizontal arm of the recording apparatus was already against the electromagnet controlled by this door. As the mouse proceeded on its way, it pushed open the door leading to the other compartment, thus closing the circuit to the corresponding

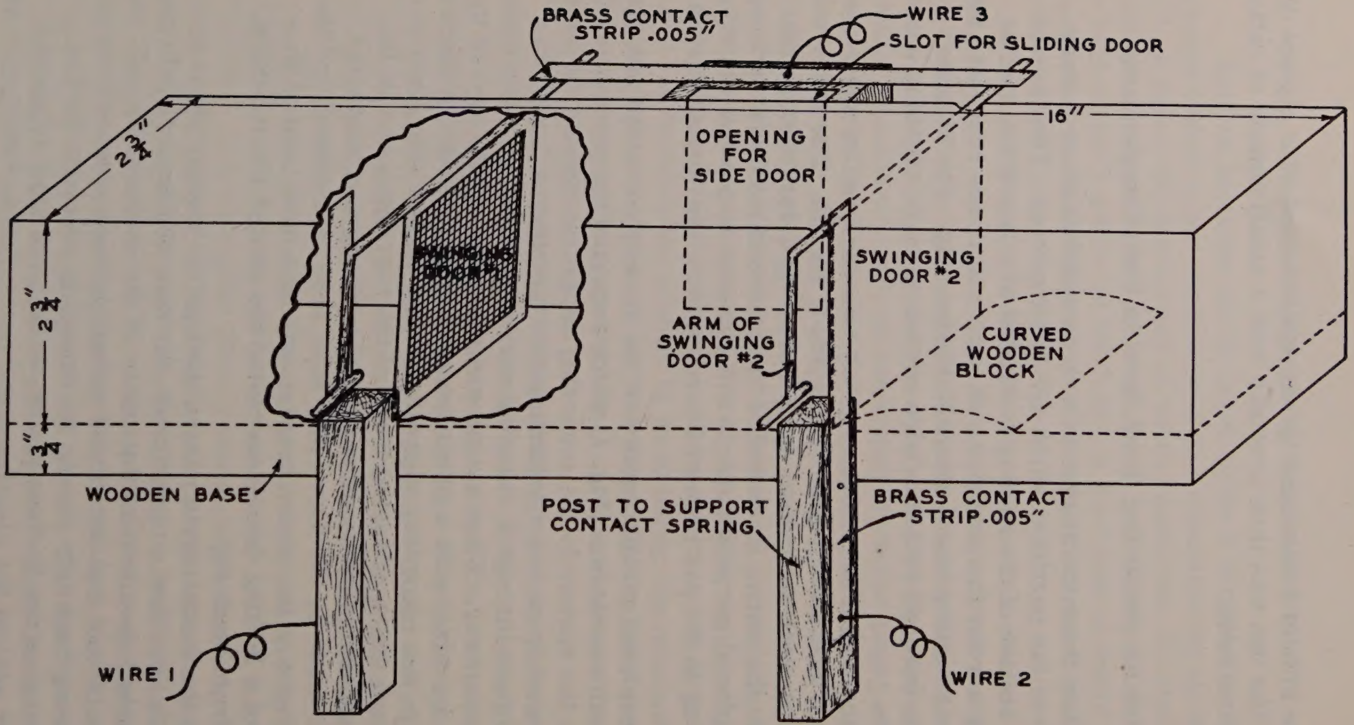

FIG. 1. Apparatus installed in the runway between the 2 compartments to record, in connection with a kymograph, the length of time the mouse remained in each compartment.

electromagnet, with the result that the horizontal arm of the recording apparatus changed its position, and the passage of the mouse was indicated.

The lines drawn by the kymograph pen attached to the end of the horizontal arm of the recording apparatus were at either of 2 horizontal levels. The upper position indicated that the mouse was in the north compartment, while the lower position indicated that the mouse was in the south compartment. The length of the line at either position, therefore, indicated the amount of time the mouse had spent in the corresponding compartment. As already explained, the position of the pen did not change until the mouse had crossed the runway and had opened the door to the compartment he was entering. If he came to the middle of the runway and then turned back, no change was made in the position of the recording pen.

The curved wooden blocks (Fig. 1) at each end of the horizontal runway forced the mouse to open the doors wide in order to pass through, and they thus insured a good electrical contact between the arm of the door and the brass strip.

The kymograph was driven by a synchronous electric motor, and its speed was reduced by 2 reducing gears to a rate which varied in the several experiments between 1 and 2 mm. per minute. The motor was started and stopped by an electric time clock which was adjusted to synchronize with the 12-hour night period in the reaction room.

Experimental Procedure

Insofar as possible, a definite procedure was followed in carrying out the experiments. Occasionally, events prevented strict adherence to this procedure, but deviations were allowed only if they seemed to be of little importance.

Conditions in the 2 compartments were kept as nearly equal as possible except for the habitat factor which was being tested. Essentially the same arrangement and distribution of the tufts of artificial grass and of the units of jungle were retained in all the experiments. For Experiment VII and subsequent experiments the distribution of the tree trunks was changed somewhat to a more regular pattern than that used in the earlier experiments.

Almost all of the mice were given a training period in order to acquaint them with the swinging doors and the activity wheels. The training periods were usually of 4 days' duration and always immediately preceded the testing period. Whether or not this training period increased the efficiency of the experiments is not known.

Training was accomplished in 2 ordinary laboratory cages connected by a runway which contained a swinging door like those in the experimental apparatus. One cage was provided with nesting material and water and the other with food and an activity wheel. This arrangement compelled the mice to pass through the runway to get the necessary food and water and a hiding place.

The first introduction of each mouse to the experimental situation was made by means of an introduction box (Pl. I, Fig. 1). This box was completely enclosed and admitted light only through a small screen door 2 by 2 1/2 inches. The door was hinged at its top and was so constructed that it could be pushed open from the inside but not from the outside. The box was placed on the partition of the reaction room and was connected with the side door of the runway apparatus by means of a screen-wire runway. After the first night of each mouse's test period, the introduction box was removed from the room.

Each mouse was tested for 4 consecutive nights. Records of the several measurements of habitat selection were taken daily in the early afternoon. This required the investigator to be present in the room for a half-hour to an hour. In general, the mice were not active during the daylight period unless disturbed by the record taking. The disturbance caused by record taking and by changing used nest boxes sometimes caused a mouse to run from compartment to compartment. A disturbed mouse was always allowed to remain wherever it was when the investigator left the room. There is no evidence that this disturbance had an effect on habitat selection in the experiments.

After each mouse was tested, the sand on the floor of the compartments was mixed and smoothed with a brush, and the activity wheels, nest boxes, food dishes, and water tubes and racks were washed in water. Between experiments the sand was sifted to remove mouse droppings and other debris. A clean nest box was substituted each day for the one used by the mouse, and the activity wheels were interchanged daily so that a particular wheel was placed in each compartment on alternate nights. Artificial habitats were changed from one compartment to the other at least once during each experiment following Experiment III. The significance of these procedures will be discussed below.

To maintain as nearly natural conditions as possible, the time clock was set to give approximately a 12-hour period of bright light and a similar period of dim light or darkness. Two 200-watt bulbs in each compartment supplied illumination during the period of bright light, which lasted approximately from 7:00 A.M. to 7:00 P.M. Dim light, when provided during the "night," was given by a 7-watt frosted bulb in the central light fixture of each compartment. A single sheet of typewriter paper covered the opening of each fixture. The illumination thus provided approximated 0.01 foot-candle when read on the floor directly beneath the light. This illumination is of about half the intensity of the light given by the zenithal full moon (Smithsonian Instit., 1918:218). The values varied somewhat from this figure, depending on the age of the bulbs and the voltage of the current. The light intensities were measured with a Weston Illumination Meter, Model 603, in the manner described by Dice (1945).

Occasionally one of the electric-light bulbs in the room burned out during an experiment. A single 200-watt bulb was discovered to be out on 9 different days during the experiments. The records show that this possibly caused an effect in the case of only 2 of 9 mice involved, both in Experiment V. Seven-watt bulbs burned out twice in the experiments, apparently without causing any effect on the reaction of the mice to the artificial habitats.

For habitat selection to occur in these experiments, it was necessary that the animal be acquainted with the alternatives to be selected. Almost all of the mice entered both compartments during the first night of their tests. If a particular mouse did not do this, a basis for habitat selection did not exist, and the data secured from that mouse were not used. Mice that did not enter both compartments during the first night of testing were not used again in any experiment.

Experimental Animals

Peromyscus maniculatus, the species studied in these experiments, ranges over most of North America from the limits of tree growth in Canada southward into southern Mexico and from the Atlantic to the Pacific Coast (Osgood, 1909). Subspecies of P. maniculatus live in many habitats within this range. The races gracilis and bairdi are excellent experimental animals for a study of habitat selection, since they show contrasting habitat preferences.

P. m. bairdi, the prairie deermouse, inhabits prairies, open fields, and lake beaches, as numerous ecological surveys have established (Wood, 1910; Dice, 1925). It is closely limited to open habitats and is rarely caught in woodland or in brushland (Wood, 1910; Blair, 1940). By extensive trapping in cultivated fields in central Missouri, I found that the catch of prairie deermice diminished to zero as the trap lines approached woody or brushy field borders. Yet this subspecies has been known to live in fields surrounded by woods, where it must presumably have passed through the woods in its dispersal movements (Howard, 1949).

The typical habitat of P. m. gracilis is the northeastern hardwood forest (Hooper, 1942), but it is also found in shrubby areas (Dice and Sherman, 1922) and in forest plantations where the trees are widely spaced and only a few feet tall (unpublished records of the author). It is thus apparently somewhat less strictly limited to the forest habitat than is the prairie deermouse to open fields.

As a consequence of deforestation and land cultivation, the prairie deermouse has extended its range eastward and northeastward (Hooper, 1942). It has thereby come into contact at some places with the forest deermouse. Both races occurred in one part of Charlevoix County, Michigan, without any evidence of intergradation (Dice, 1931a). In the laboratory, however, they will interbreed, and their F_1 hybrids of both sexes are fertile (Dice, 1933).

The mice used in these experiments were taken from the stocks of the Laboratory of Vertebrate Biology. In the laboratory they were given the same care received by all the mice (Dice, 1929). The P. m. bairdi stock, called Washtenaw in the laboratory records, was reared from individuals caught in fields about 3 miles west of the University. Some of the original field-caught individuals were tested in the first 3 experiments, but laboratory-born stock was employed in the remaining experiments. The field-caught P. m. gracilis specimens were obtained from a wooded area 1 mile east of Munising, Michigan. These are recorded as the Cusino stock in the laboratory but were later added to the Pine Lake stock of gracilis. The Pine Lake stock was reared from mice obtained in 1940 from the Cusino Wildlife Refuge, Munising, Michigan.

Although it was not possible to select mice of exactly the same age, only sexually mature and apparently normal individuals were used. Among the laboratory-bred mice the oldest mouse tested was 84 weeks of age and the youngest was 22 weeks old. Most were between 7 and 19 months. The ages of the field-caught individuals used in part of the first 3 experiments were, of course, unknown.

STATISTICAL ANALYSIS

The time required to test each mouse limited the number of mice that could be tested in a single experiment. Approximately 8 individuals of each race were tested in every experiment except those in which a clear-cut difference in artificial-habitat selection was apparent with fewer individuals.

The data are analyzed statistically by 2 methods. (1) Analysis of variance which employs the F test of significance (Snedecor, 1946:218) was used to evaluate the data for habitat selection as measured by the numbers of turns of the activity wheels, numbers of seeds eaten, and amounts of water consumed. (2) Comparison of means by the t test of significance (Snedecor, 1946:42) was employed to analyze the measurement of time spent in the artificial habitats.

Analysis of Variance

For the analysis of variance the data for each measurement were fitted to a 2 by 4 by n table which permitted comparison with the experimental error (F) of variations between the 2 habitats, of variations among the 4 days for the same mouse, and of variations among n mice. The significance of interactions between any 2 of these variations was also computed in the analysis. Whenever these interactions were not statistically significant, they were combined with the experimental error. The new F values derived are presented in the tables. Interactions between individual mice and days and between habitats and days were often combined with experimental error in the calculations.

It has already been explained that the count of seeds eaten was a close estimate and not a precise count. Estimated data may be analyzed statistically in the same way as exact data if the method of estimation does not bias the collection of the data. The results of statistical analysis for estimated data are no more accurate than the data.

Certain special cases pertaining to the calculation of the data by analysis of variance should be mentioned. A male P. m. bairdi was accidentally killed on the third day of observation in Experiment IV. The records for the fourth night were estimated by the formula for estimation of missing values. Another special case concerns the recording of certain data when observations were not made on 1 day. The amount of water supplied the mice in each habitat and the possible number of revolutions which could be recorded on the counter of an activity wheel were large enough not to be exceeded by the amount of water used or the number of turns on the wheel made by a mouse during a 2-day period. Rather than omit the data and replace it by estimation, readings were divided equally between those 2 days. This was done for 1 mouse in each of the following cases: bairdi, Experiment IV, wheel and water, second and third days; gracilis, Experiment VI, water, third and fourth days; and bairdi, Experiment VI, water, third and fourth days.

Items of data were occasionally not recorded because of oversight or conditions which prevented their being obtained. In order to use analysis of variance in a 3-way table, it is necessary to supply the missing table entries. A theory for the estimation of missing data has been developed (Goulden, 1939:261; Cochran and Cox, 1950:72), but the particular application needed here was not readily available. According to this theory, estimates are derived which minimize the error sum of squares. One degree of freedom is subtracted from the degrees of freedom associated with the error sum of squares for each estimated missing value. Dr. C. C. Craig supplied the specific formula used in these calculations. Since a description of this formula (Harris, 1950) is rather involved and applies only to the specific experimental design used here, it will not be repeated.

The data for numbers of seeds eaten and the amount of water consumed by males and females in each experiment were studied by analysis of variance to determine if a sexual difference in habitat selection occurred. The calculations were made separately for each of the 2 subspecies of Peromyscus. The daily records for each mouse in each artificial habitat were added, and the resulting values for one artificial habitat were subtracted from the corresponding values for the other artificial habitat. Thus, the reaction of each mouse to the 2 habitats was represented by a single value which was the difference between the 2 values for the 2 habitats in each experiment. The single values for male individuals in an experiment were then compared with the single values for the females by obtaining the ratio of variation between sexes to variation within sexes.

Comparison of Means

In the data for the amount of time spent in each of the 2 habitats, more than 5 missing table entries (a number arbitrarily chosen) sometimes occurred because of failure of the apparatus. As the number of missing values that must be supplied increases, the precision of the analysis of variance decreases. Another method of analysis, therefore, was advisable for the measure of time.

The number of minutes spent by a mouse in one habitat was directly related to the number of minutes spent in the other habitat.

Thus, the method used here is adapted to small samples in which values are paired and correlated (Smith and Duncan, 1945:403). The number of minutes spent each night by the mice in one habitat was subtracted from the number of minutes spent in the other habitat, and a t test of the difference of the subtracted values from zero was obtained. If there were no difference between the times spent by the mice in the 2 habitats, the total of the subtracted values would equal zero. It is to be noted that variation among daily records of each mouse was lost in this method of analysis. Each daily record was treated as though it were obtained from a different mouse. By eliminating variation among daily records of each mouse, this method of analysis becomes less precise than the method employed for the other measurements of habitat selection.

The correction of certain inaccuracies in the time record should be noted since they involve the data which are treated statistically. The period during which each nightly record was taken was regulated by time clock, and the lengths of the lines produced on the kymograph paper during these periods should always have been the same. Actually, they varied by several millimeters from day to day. This variation was eliminated by converting the time record from millimeters to minutes, the length of each day's line forming the basis of the conversion factor for that day. In this way the proportion of time spent by a mouse in each habitat and the total amount of time recorded each day were retained.

From the description of the runway apparatus it is evident that in certain circumstances an exact record of the time spent by a mouse in each habitat may not have been obtained. A mouse, after being in 1 habitat, could return to the center of the runway apparatus between the doors and remain there while still being recorded as present in the habitat which it had just left. This could also occur at the beginning and end of the mouse's activity periods during each night. These possible errors are assumed to be randomized between habitats and among the mice in each experiment.

When a mouse was released into the introduction box at the beginning of its 4-day testing period, the horizontal arm of the recording apparatus was placed halfway between the magnets. If the mouse did not become active until after the kymograph began to operate, a known period of time occurred during which the mouse was in neither artificial habitat. Similar periods of time could occur at the beginning and end of each of the other 3 nights as described in the preceding paragraph, but their occurrence and length were unknown. To omit the known period during which the mouse was inactive would again introduce a variation in the time record. For this reason the known period of time during which the mouse was in neither habitat at the beginning of the first night was divided between the habitats in the same proportion that occurred for the active part of the night.

DESCRIPTIONS AND RESULTS OF THE EXPERIMENTS

Descriptions of the precise conditions for each experiment, together with the results, are given here. The term "significant" in this section refers to significance in the statistical sense. The initials "d.f." signify degrees of freedom. The original data of these experiments and the tables recording the complete analyses of variance are given in the microfilm publication (Harris, 1950).

Experiment I

The reactions of the 2 subspecies of deermice, Peromyscus maniculatus gracilis and P. m. bairdi, to the tree-trunk and to the artificial-grass habitats were tested in this experiment. Cardboard disks were fastened to the tops of the tree trunks to produce shade simulating that caused by the foliage of natural trees. The tufts of artificial grass, 142 in number, were spaced 5 inches apart on the laths. Dim lights (approximately 0.01 foot-candles) produced illumination during the night period. A Petri dish containing 40 sunflower seeds was placed in each compartment. The artificial habitats were not changed from one compartment to the other during the experiment. Since guards were not present around the entrance to the horizontal section of the runway, it was possible for mice to go from compartment to compartment without passing through the section of the runway carrying the contact mechanism. A few gracilis did jump from the slanting part of the runway to the divisional wall and from there climbed to various nooks and crannies above the floor of the room.

Six male and 2 female bairdi and 4 male and 4 female gracilis were tested. All except 1 male bairdi and 2 male gracilis were field caught.

The F values computed by analysis of variance for 3 of the 4 measurements of habitat selection in this experiment are given in Table I. Total values for all 4 measurements are found in Table II. The difference between the mean times spent in the 2 artificial

TABLE I

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment I.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	4.41** (7;45)†	7.05** (7;43)	4.09** (7;42)	1.29 (7;43)	3.08* (7;43)	0.69 (7;43)
Between habitats	4.66* (1;45)	1.38 (1;43)	3.29 (1;42)	8.01** (1;43)	138.27** (1;43)	0.17 (1;43)
Among days	1.18 (3;45)	3.15* (3;43)	2.25 (3;42)	1.44 (3;43)	0.88 (3;43)	2.15 (3;43)
Interaction: habitats x individuals	2.09 (7;45)	10.31** (7;43)	7.73** (7;42)	2.93* (7;43)	14.38** (7;43)	5.54** (7;43)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 degrees of freedom; n_2 degrees of freedom.

TABLE II

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment I. Values are estimated for 11 items of missing data.

	8 gracilis		8 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes	11353††	9227	5554	9146†
Per cent	55.2††	44.8	37.8	62.2†
Activity wheels				
Total turns	106701†	29171	103281	65822
Per cent	78.5†	21.5	61.1	38.9
Seeds eaten				
Total seeds	621	511	342	558††
Per cent	54.9	45.1	38.0	62.0††
Water consumed				
Total ml.	65.8††	17.9	35.6	33.2
Per cent	78.6††	21.4	51.7	48.3

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

habitats by gracilis is significant at the 1 per cent level ($t = 11.00$ with 27 d.f.), and by bairdi is significant at the 5 per cent level ($t = 2.53$ with 19 d.f.).

P. m. gracilis scored higher total values in the tree-trunk habitat than in the artificial-grass habitat in all 4 measurements of habitat selection. The tendency of gracilis to select the tree-trunk habitat is indicated by the significant difference between the 2 habitat means in each of 3 measurements: time, activity wheel, and water.

For bairdi, higher total values were obtained in the artificial-grass habitat than in the tree-trunk habitat in 2 of the 4 measurements of habitat selection. Significant differences between habitat means in these 2 measurements — time and seeds — show a tendency for bairdi to prefer the artificial-grass habitat.

In Experiment I, however, 2 variables were present: (1) Artificial habitats composed of tree trunks and of artificial grass presented vegetational differences. (2) The intensity of light differed on the floors of the compartments beneath the 2 artificial types of vegetation. This was true because the cardboard disks on the tree trunks produced more shade than the narrow strips of paper forming the artificial grass, so that, in general, the floor of the tree-trunk compartment was darker than that of the artificial-grass compartment.

Experiments II and III

Experiments II and III were designed to determine if light intensity affected artificial-habitat selection. The artificial habitats in these 2 experiments were the same as those in Experiment I. In Experiment II the intensity of the night light in the artificial-grass compartment was lowered from approximately 0.01 foot-candle to 0.0042 foot-candle by placing 4 sheets of typewriter paper over the opening of the central light fixture. Two male and 1 female gracilis and 3 male bairdi were tested. All had been previously used in Experiment I.

In Experiment III the night light in the tree-trunk compartment was reduced to 0.0038 foot-candle by 4 sheets of typewriter paper. A burlap curtain was dropped above the partition to further differentiate the intensities of light on the floors of the 2 compartments. It should be mentioned that the curtain interfered with air circulation and produced a difference in temperature of as much as 8° F. between the 2 compartments, the tree-trunk compartment being the cooler. Three male gracilis and 3 male bairdi were tested. All except 1 male bairdi had previously been used in Experiments I or II or in both.

The data from these experiments were not treated statistically. In spite of the few mice tested, the gross results seem to indicate that light intensity may have been a factor influencing selection of the artificial habitats. The preference for the artificial-grass habitat shown by bairdi appeared to be strengthened, as compared with Experiment I, when the light intensity in the artificial-grass compartment was reduced, and was weakened when the light intensity of the tree-trunk compartment was reduced. A preference for the artificial-grass habitat was indicated by gracilis in the measurements of total time and activity-wheel turns when the light intensity was reduced in the artificial-grass compartment, and a weaker selection of the tree-trunk habitat was indicated by the measurements of seeds eaten and water drunk. The preference for tree trunks exhibited by gracilis seemed to be strengthened somewhat when the light intensity in the tree-trunk compartment was reduced.

Experiment IV

Light intensity on the floor beneath the artificial vegetation proved very difficult to measure precisely, and no adequate control of it could be devised. This factor was eliminated in Experiment IV by using no lights at all during the night period.

Since the cardboard disks now served no function, they were removed from the tree trunks. Tree-trunk and artificial-grass habitats were arranged as in the preceding experiments, and each was changed once from one compartment to the other during the experiment. Four male and 3 female gracilis and 3 male and 4 female bairdi were tested. All of these mice were laboratory bred and none had been previously tested.

The F values obtained from the analysis of variance of 3 measurements of habitat selection in Experiment IV are given in Table III. The totals of values obtained in all the measurements are recorded by habitat in Table IV. No significant difference occurred between the mean times spent by gracilis in the 2 artificial habitats ($t = 0.68$ with 20 d.f.). More time was spent by bairdi in the artificial-grass habitat, and the difference between mean times was significant at the 1 per cent level ($t = 9.65$ with 20 d.f.).

Values obtained in the tree-trunk habitat for gracilis were

TABLE III

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment IV.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	11.49** (6;39)†	10.73** (6;20)	1.19 (6;39)	1.45 (5;28)	0.55 (6;39)	5.05** (6;39)
Between habitats	4.70* (1;39)	5.79* (1;20)	25.70** (1;39)	64.97** (1;28)	188.36** (1;39)	122.00** (1;39)
Among days	0.82 (3;39)	3.68* (3;20)	0.16 (3;39)	0.09 (3;28)	0.30 (3;39)	0.61 (3;39)
Interaction: habitats x individuals	4.20** (6;39)	5.86** (6;20)	4.68** (6;39)	4.59** (5;28)	5.64** (6;39)	6.52** (6;39)
Interaction: days x individuals . .	. . . .	2.33* (18;20)	. . . . .	. . . .	. . . .	. . . .

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE IV

Summary of Selection by Peromyscus maniculatus gracilis and P.m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment IV. Values are estimated for 6 items of missing data.

	7 gracilis		7 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes . . .	8297	7432	2219	13510††
Per cent.	52.7	47.3	14.1	85.9††
Activity wheels				
Total turns	10936†	5896	37357	74234†
Per cent.	65.0†	35.0	33.5	66.5†
Seeds eaten				
Total seeds	764††	409	199	686††
Per cent.	65.1††	34.9	22.5	77.5††
Water consumed				
Total ml.	86.6††	27.6	23.8	82.0††
Per cent	75.8††	24.2	22.5	77.5††

†Represents a value significant at the 5 per cent level.
††Represents a value significant at the 1 per cent level.

greater than those obtained in the artificial-grass habitat, and the differences between mean values in the 2 habitats were significant in 3 measurements: wheel turns, seeds, and water. This indicates a preference for the tree-trunk habitat by gracilis. For bairdi differences between mean values in the 2 artificial habitats were significant in all 4 measurements. The greater of each pair of mean values was obtained in the artificial-grass habitat for each measurement, revealing the selection of that habitat by bairdi.

Experiment V

Habitat selection might theoretically occur either as a positive reaction toward certain features of the habitat selected or as a negative reaction against certain features of the habitat avoided. To gain information about these possibilities, in Experiment V the mice were offered habitats differing in only 1 feature of artificial vegetation. The tree-trunk habitat contained artificial grass in addition to the tree trunks, and it was contrasted with a habitat in which only artificial grass was present.

The arrangement of the tufts of artificial grass was closely similar in the 2 habitats; 98 tufts were used in the tree-trunk habitat and 102 tufts in the artificial-grass habitat. The tufts were spaced at 7-inch intervals on the laths in both compartments. Artificial habitats were changed from one compartment to the other once during the experiment. Dim lights were used during the night period since the intensity of light reaching the floor was nearly equal in the 2 compartments, differing only in the shadows cast by the tree trunks. Finger bowls for the sunflower seeds replaced the Petri dishes of previous experiments. Three male and 5 female gracilis and 4 male and 5 female bairdi were tested. None of these individuals had been tested in previous experiments.

In Tables V and VI, respectively, are found the F values for 3 measurements of artificial-habitat selection and the total values obtained for all measurements. The difference between mean times spent by gracilis in the 2 artificial habitats was significant at the 1 per cent level (t = 2.96 with 29 d.f.). There was no significant difference in the mean times spent by bairdi in the 2 habitats (t = 0.88 with 23 d.f.).

The tree-trunk and artificial-grass habitat was selected by gracilis in this experiment, as evidenced by the mean values which were higher in this habitat than in the artificial-grass habitat for all 4 measurements of habitat selection. The differences between

TABLE V

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment V.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	16.77** (7;21)†	2.87** (8;59)	0.59 (7;45)	1.21 (8;51)	0.71 (7;45)	1.54 (8;51)
Between habitats	0.10 (1;21)	5.66* (1;59)	18.51** (1;45)	5.88* (1;51)	15.74** (1;45)	3.11 (1;51)
Among days	2.00 (3;21)	2.43 (3;59)	0.06 (3;45)	0.61 (3;51)	1.23 (3;45)	1.06 (3;51)
Interaction: habitats x individuals	6.43** (7;21)	. . . .	3.72** (7;45)	3.37** (8;51)	2.71* (7;45)	7.67** (8;51)
Interaction: days x individuals . . .	2.36* (21;21)	. . . .	. . . .	. . . .	. . . .	. . . .
Interaction: habitats x days	3.56* (3;21)	. . . .	. . . .	. . . .	. . . .	. . . .

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE VI

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between the Tree-trunk with Artificial-grass Habitat and the Artificial-grass Habitat in Experiment V.

	8 gracilis		9 bairdi	
	Tree + Grass	Grass Only	Tree + Grass	Grass Only
Presence in habitat				
Total minutes	14570††	7900	9977	12493
Per cent	64.8††	35.2	44.4	55.6
Activity wheels				
Total turns	94183	87599	98893	198212†
Per cent	51.8	48.2	33.3	66.7†
Seeds eaten				
Total seeds	737††	358	439	642†
Per cent	67.3††	32.7	40.6	59.4†
Water consumed				
Total ml.	60.0††	35.0	42.4	53.2
Per cent	63.2††	36.8	44.4	55.6

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

mean values in the 2 habitats were significant at the 1 per cent level for 3 of the 4 measurements of habitat selection: time, seeds, and water.

No significant selection was made by bairdi for either of the 2 artificial habitats. Although the mean values obtained in the artificial-grass habitat were higher than those obtained in the tree-trunk and artificial-grass habitat, their differences were significant at the 5 per cent level for only 2 measurements: wheel turns and seeds. A considerable number of seeds in addition to those eaten was removed from the food dish and stored by the individuals of bairdi tested, and the mean values of seeds removed in the 2 habitats were not significantly different.

Experiment VI

In Experiment VI a jungle in one compartment opposed artificial grass in the other compartment. The jungle was arranged to cover the floor space almost completely, except for an aisle along 1 side of the compartment. The artificial-grass habitat remained as in previous experiments. No lights were used in the night period. During the experiment the artificial habitats were changed once from one compartment to the other. Five male and 3 female gracilis and 5 male and 3 female bairdi were tested. One female gracilis had been previously tested in Experiment V.

Aside from the form of the artificial vegetation, the tree-trunk habitat presented in these experiments 2 additional features that might be important in artificial-habitat selection. The floor of the tree-trunk compartment, as in Experiment IV, had little cover for the mice in comparison with that of the artificial-grass compartment. Also, the tree trunks themselves afforded an opportunity for gracilis to climb about, as it probably does in nature. These 2 features, in the absence of tree trunks, were presented by the jungle which, in a highly stereotyped manner, simulated a brushy habitat.

Table VII presents the F values obtained in the statistical analysis of 3 measurements of artificial-habitat selection. The total values for all 4 measurements are given in Table VIII. There was no significant difference between mean times spent by gracilis in the 2 artificial habitats ($t = 0.39$ with 30 d.f.). The mean time spent by bairdi in the artificial-grass habitat was significantly greater at the 1 per cent level ($t = 3.31$ with 30 d.f.) than that spent in the jungle habitat.

TABLE VII

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment VI.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	8.29** (7;43)†	4.52** (7;45)	1.65 (7;43)	4.45** (7;40)	2.72* (7;45)	1.10 (7;45)
Between habitats	1.26 (1;43)	0.43 (1;45)	17.36** (1;43)	16.07** (1;40)	1.56 (1;45)	10.74** (1;45)
Among days	0.56 (3;43)	0.83 (3;45)	1.01 (3;43)	0.62 (3;40)	0.26 (3;45)	1.50 (3;45)
Interaction: habitats x individuals	1.87 (7;43)	5.80** (7;45)	12.15** (7;43)	7.04** (7;40)	3.90** (7;45)	4.76** (7;45)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE VIII

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Jungle and Artificial-grass habitats in Experiment VI. Values are estimated for 9 items of missing data.

	8 gracilis		8 bairdi	
	Jungle	Grass	Jungle	Grass
Presence in habitat				
Total minutes	11231	11988	8345	14874††
Per cent........	48.4	51.6	35.9	64.1††
Activity wheels				
Total turns	61025	32842	63021	79047
Per cent	65.0	35.0	44.4	55.6
Seeds eaten				
Total seeds	867††	577	323	606††
Per cent........	60.0††	40.0	34.8	65.2††
Water consumed				
Total ml.	61.6	53.6	35.0	52.0††
Per cent........	53.5	46.5	40.2	59.8††

†† Represents a value significant at the 1 per cent level.

In this experiment no definite preference was shown by gracilis for either artificial habitat. Higher mean values were obtained in the jungle habitat than in the artificial grass for 3 measurements: wheel turns, seeds, and water. The differences between mean values in the 2 habitats were significant only for seeds eaten.

On the other hand, bairdi showed a preference for the artificial-grass habitat. This preference was manifested by higher mean values in the artificial-grass than in the jungle habitat for all 4 measurements. The differences between mean values of the 2 habitats were significant at the 1 per cent level for 3 of the measurements: time, seeds, and water.

Experiments VII and IX

As a crucial test for the positive selection of tree trunks by gracilis, tree trunks were contrasted with jungle as the artificial habitats used in Experiment VII. The tree trunks and jungle were arranged in the 2 compartments as in previous experiments. No lights were used during the night period. In this and the following experiments 45 sunflower seeds were placed daily in each food dish. The habitats were changed from compartment to compartment after each 2 mice were tested. Four male and 4 female gracilis were used; of these, 2 males and 2 females had been tested in previous experiments.

Experiment IX repeated Experiment VII, testing 3 male and 3 female gracilis, all but one of which were individuals not tested in Experiment VII. In Experiment IX the ventilating fan at one end of the room was turned off. Heat was provided by an electric heater with a circulating fan which was placed over one end of the partition. An electric fan was placed on the other end of the partition to aid in the circulation of warm air. The air currents produced by the fans caused no movement of the artificial grass.

The results of statistical analysis of 3 measurements of habitat selection in Experiments VII and IX are given as F values in Table IX. In Table X are recorded by habitat the total values of all 4 measurements in the 2 experiments. Differences between mean times spent by gracilis in the 2 artificial habitats were not significant in either experiment ($t = 1.00$ with 31 d.f. for Experiment VII and $t = 0.91$ with 21 d.f. for Experiment IX).

In Experiment VII a tendency was shown by gracilis to choose the jungle habitat in preference to the tree-trunk habitat.

TABLE IX

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis in Experiment VII and in Experiment IX.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	VII	IX	VII	IX	VII	IX
Among individuals	12.23** (7;20)†	5.03** (5;31)	1.74 (7;45)	1.82 (5;31)	1.17 (7;45)	3.59* (5;33)
Between habitats	8.23** (1.20)	0.67 (1;31)	14.89** (1;45)	1.16 (1;31)	12.81** (1;45)	0.03 (1;33)
Among days	0.63 (3;20)	1.64 (3;31)	0.21 (3;45)	0.09 (3;31)	0.79 (3;45)	0.21 (3;33)
Interaction: habitats x individuals	5.46** (7;20)	0.56 (5;31)	10.27** (7;45)	1.10 (5;31)	3.91** (7;45)	4.44** (5;33)
Interaction: days x individuals . . .	3.57** (21;20)	. . . .	. . . .	. . . .	. . . .	. . . .

*Value is significant at the 5 per cent level.

**Value is significant at the 1 per cent level.

† n_1 d.f.; n_2 d.f.

TABLE X

Summary of Selection Between Jungle and Tree-trunk Habitats by 8 Peromyscus maniculatus gracilis in Experiment VII and by 6 P. m. gracilis in Experiment IX. Values are estimated for 4 items of missing data in each experiment.

	Experiment VII		Experiment IX	
	Tree	Jungle	Tree	Jungle
Presence in habitat				
Total minutes	11024	12944	8851	7627
Per cent.	46.0	54.0	53.7	46.3
Activity wheels				
Total turns	31696††	14502	30338	32496
Per cent	68.6††	31.4	48.3	51.7
Seeds eaten				
Total seeds.	549	815††	401	458
Per cent	40.2	59.8††	46.7	53.3
Water consumed				
Total ml.	57.4	83.8††	48.6	47.8
Per cent.	40.7	59.3††	50.4	49.6

†† Represents a value significant at the 1 per cent level.

The mean values obtained in the jungle habitat were higher than those obtained in the tree-trunk habitat for 3 measurements, and the differences between mean values of the 2 habitats were significant at the 1 per cent level for 2 measurements, seeds and water. For the fourth measurement, wheel turns, the higher value of the 2 occurred in the tree-trunk habitat, and the difference between means was significant at the 1 per cent level. In Experiment IX, however, with somewhat different but more equal experimental conditions, no significant selection was exhibited by gracilis. The total values in the 2 habitats for each measurement were close to equality, and the higher of the 2 habitat values occurred in the tree-trunk habitat for 2 measurements and in the jungle for the other 2 measurements.

Experiment VIII

It is evident from Experiment IV, in which no lights were present during the night period, that habitat selection by gracilis and by bairdi occurs in the absence of visual stimuli. Experiment VIII was designed to test the hypothesis that perception of the artificial habitat may be received through the vibrissae. Three male and 1 female gracilis and 3 male and 3 female bairdi were tested. Of these mice, a male gracilis and a male and a female bairdi had not been tested in previous experiments. If vibrissae are the sensory structures largely used in the selection of habitat, their removal from animals already tested would provide a crucial test. The mice were given the usual 4-day period of training. Each mouse was then etherized and the vibrissae were clipped close to the skin. After the mouse had fully recovered from the ether, it was released in the introduction box.

The artificial habitats presented for selection by the mice were tree trunks in one compartment and artificial grass in the other. Individual mice of the 2 subspecies were not tested alternately. Artificial habitats were changed from one compartment to the other once for each subspecies. As in Experiment IX, accessory fans were used in place of the one built into the air duct of the reaction room.

In Table XI are recorded the F values computed by analysis of the data obtained for 3 measurements of habitat selection. Table XII presents the total values by habitat for all 4 measurements. The difference between the mean values of time spent by gracilis in the 2 artificial habitats is significant at the 1 per cent

TABLE XI

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment VIII.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	8.13** (3;21)†	10.23** (5;33)	0.77 (3;18)	1.78 (5;33)	3.16* (3;21)	1.39 (5;33)
Between habitats	4.78* (1;21)	1.78 (1;33)	85.58** (1;18)	7.45** (1;33)	42.71** (1;21)	25.09** (1;33)
Among days	1.91 (3;21)	1.77 (3;33)	1.97 (3;18)	0.30 (3;33)	1.43 (3;21)	2.05 (3;33)
Interaction: habitats x individuals	5.21** (3;21)	6.79** (5;33)	3.84** (3;18)	2.83* (5;33)	6.73** (3;21)	12.46** (5;33)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
†n_1 d.f.; n_2 d.f.

TABLE XII

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment VIII. The vibrissae of the mice had been artificially removed. Values are estimated for 3 items of missing data.

	4 gracilis		6 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes	8035††	3200	6846	9992
Per cent.	71.5††	28.5	39.4	60.6
Activity wheels				
Total turns	1555	3870†	43231	65815
Per cent.	28.7	71.3†	39.6	60.4
Seeds eaten				
Total seeds.	561††	139	277	454††
Per cent.	80.1††	19.9	37.9	62.1††
Water consumed				
Total ml.	52.0††	25.6	37.6	63.8††
Per cent	67.0††	33.0	37.1	62.9††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

level (t = 5.19 with 14 d.f.). No significant difference occurred between the 2 mean values of time spent by bairdi in the 2 habitats (t = 1.94 with 21 d.f.).

The results of this experiment indicate that gracilis selected the tree-trunk habitat even though the individuals tested were deprived of their vibrissae. A significant difference at the 1 per cent level occurred between habitat means for 3 measurements — time, seeds, and water — with the higher of the 2 means for each measurement occurring in the tree-trunk habitat. For the measurement of activity-wheel turns the higher of the 2 habitat means occurred in the artificial-grass habitat, and the difference was significant at the 5 per cent level.

Vibrissaeless bairdi showed a tendency to select the artificial-grass habitat. Mean values obtained in this habitat were higher than those obtained in the tree-trunk habitat. For 2 measurements — seeds and water — the differences between habitat means were significant at the 1 per cent level. The selection of the artificial grass by vibrissaeless bairdi was not so strong as that by bairdi with vibrissae intact in Experiment IV.

Experiment X

Since bairdi and gracilis produce fertile offspring in the laboratory (Dice, 1933) but apparently do not do so in nature (Dice, 1931a), artificial-habitat selection by their F_1 hybrids might be expected to furnish interesting information. Four male and 3 female F_1 hybrids of a bairdi x gracilis cross were tested in Experiment X for their selection between tree trunks and artificial grass. All 3 females were pregnant at the time of testing. The ventilating fan of the reaction room was turned off. No night lights were used during the tests. The artificial habitats were changed twice from one compartment to the other during the experiment.

F values computed by analysis of variance for 3 measurements of habitat selection in Experiment X are presented in Table XIII. Total values recorded by habitats for all measurements are given in Table XIV. The difference between mean times spent by the hybrids in the 2 artificial habitats is significant at the 1 per cent level (t = 3.72 with 20 d.f.).

The F_1 hybrids of bairdi x gracilis selected the artificial-grass habitat. The means obtained in this habitat for all measurements of habitat selection were higher than those obtained in the tree-trunk habitat, and the differences between means in the 2

TABLE XIII

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus bairdi x P. m. gracilis F_1 in Experiment X.

Source of Variation	Numbers of Revolutions Made in Activity Wheels	Numbers of Seeds Eaten	Milliliters of Water Consumed
Among individuals	4.98** (6;37)†	3.84** (6;45)	11.71** (6;36)
Between habitats	4.28* (1;37)	12.54** (1;45)	38.49** (1;36)
Among days	2.31 (3;37)	1.49 (3;45)	1.42 (3;36)
Interaction: habitats x individuals	2.72* (6;37)	. . . .	2.82* (6;36)
Interaction: days x habitats	. . . .	. . . .	7.56** (3;36)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE XIV

Summary of Selection by 7 Peromyscus maniculatus bairdi x P. m. gracilis F_1 Between Artificial-grass and Tree-trunk Habitats in Experiment X. Values are estimated for 4 items of missing data.

	Tree	Grass
Presence in habitat		
Total minutes	5057	10654††
Per cent	32.3	67.7††
Activity wheels		
Total turns	49190	94545†
Per cent	34.2	65.8†
Seeds eaten		
Total seeds	440	754††
Per cent	36.9	63.1††
Water consumed		
Total ml.	61.6	107.8††
Per cent	36.4	63.6††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

habitats were significant at the 1 per cent level for all measurements except activity-wheel turns. In the latter instance, significance occurred at the 5 per cent level.

Artificial Habitats Selected

When the experiments described above are considered as a whole, it is noted that each subspecies usually selected the artificial habitat which simulated its natural habitat.

P. m. gracilis, the forest deermouse, showed a definite preference for the tree trunks when this habitat opposed the artificial grass in Experiments I, IV, V, and VIII. This selection was indicated by the mean values of the 4 measurements of habitat selection which, with 1 exception, were higher in the tree-trunk habitat than in the artificial grass. In each of these experiments 3 of the 4 measurements exhibited statistically significant differences between habitat means. In all of these experiments statistical significance occurred in 13 of the 16 measurements. In 10 measurements differences between habitat means were significant at the 1 per cent level and in 3 measurements, at the 5 per cent level. Of the latter, the measurement of wheel turns constituted the exception in which the higher of the 2 habitat means was in the artificial grass (Table XV). In Experiment I the selection was somewhat weaker than in the other experiments, in that the difference between the numbers of seeds eaten in the 2 habitats was not statistically significant. In this experiment, however, dim lights during the night periods caused unequal intensities of illumination on the floor of the 2 compartments.

P. m. gracilis did not respond in a consistent manner when jungle was opposed either to tree trunks or to artificial grass. In Experiment VI a tendency was shown to select the jungle habitat rather than the artificial-grass habitat, but in only 1 measurement was this preference statistically significant (Table XV); therefore, this weak habitat preference is not convincing. Jungle was also used in Experiment VII, but in contrast with tree trunks. Here, gracilis showed a preference for jungle, but the records suggest that some other factor was also involved in the choice. This experiment was repeated, therefore, as Experiment IX in an attempt to eliminate possible differences between the compartments which may have existed in addition to the differences in the habitats. There was now no preference shown by gracilis either for the jungle or for the tree trunks.

TABLE XV

Summary of Selection by Peromyscus maniculatus gracilis Between Contrasting Artificial Habitats.

Experiment	Light Intensity in f.c.	Habitat with the Higher Mean			
		Total Time in Habitat	Activity-Wheel Turns	Seeds Eaten	Water Consumed
I Tree vs. grass	0.01	tree††	tree†	tree	tree††
IV Tree vs. grass	dark	tree	tree†	tree††	tree††
V Tree + grass vs. grass	0.01	tree††	tree	tree††	tree††
VI Jungle vs. grass	dark	grass	jungle	jungle††	jungle
VII Tree vs. jungle	dark	jungle	tree††	jungle††	jungle††
VIII Tree vs. grass: mice with vibrissae removed	dark	tree††	grass†	tree††	tree††
IX Tree vs. jungle: without ventilating fan	dark	tree	jungle	jungle	tree

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

TABLE XVI

Summary of Selection by Peromyscus maniculatus bairdi Between Contrasting Artificial Habitats.

Experiment	Light Intensity in f.c.	Habitat with the Higher Mean			
		Total Time in Habitat	Activity-Wheel Turns	Seeds Eaten	Water Consumed
I Tree vs. grass	0.01	grass†	tree	grass††	tree
IV Tree vs. grass	dark	grass††	grass†	grass††	grass††
V Tree + grass vs. grass	0.01	grass	grass†	grass†	grass
VI Jungle vs. grass	dark	grass††	grass	grass††	grass††
VIII Tree vs. grass: mice with vibrissae removed	dark	grass	grass	grass††	grass††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

The results of these 3 experiments (VI, VII, and IX), when viewed together, indicate that gracilis made no consistent choice between the jungle and tree trunks or between the jungle and artificial grass. It is possible that the highly artificial nature of the jungle, which has no counterpart in natural vegetation, did not stimulate habitat selection by gracilis.

In Experiment V the tree trunks with artificial grass were selected by gracilis over the habitat with artificial grass alone (Table XV). Apparently, the presence of artificial grass together with the tree trunks did not modify the natural habitat selection for tree trunks by gracilis. Thus, it appears that attention was directed by gracilis to the tree trunks and that there was a positive selection for them. This interpretation, however, is not fully convincing in view of the lack of pronounced habitat preference shown by gracilis in Experiments VII and IX, in which the tree-trunk habitat was contrasted with jungle.

To consider only those experiments in which tree trunks and artificial grass were presented as the contrasting artificial habitats, it seems evident from the generally consistent and statistically significant results that gracilis preferred the tree-trunk habitat. There is some suggestion that this habitat selection is a positive reaction to the tree trunks, but this evidence is not completely consistent.

Table XVI shows that P. m. bairdi, the prairie deermouse, selected the artificial-grass habitat with a high degree of consistency when this was opposed either to the tree-trunk habitat or to the jungle (Experiments I, IV, VI, and VIII). The mean values resulting from the measurements were higher in the artificial grass than in the opposed habitats. Experiment I offers the only exception to this; the means obtained in the tree-trunk habitat were higher than those obtained in the contrasting artificial-grass habitat for activity-wheel turns and for water consumed. This was a preliminary experiment, however, in which the dim light used during the night period was a complicating factor.

Experiment IV, in which no light was used during the night period, was the crucial test for selection between tree-trunk and artificial-grass habitats. In this experiment bairdi selected the artificial-grass habitat as shown by significant differences between habitat means in all 4 measurements, 3 of them being significant at the 1 per cent level and 1 at the 5 per cent level. In all of these 4 experiments, in which artificial grass opposed either tree trunks or jungle, statistical significance occurred in 11 of the 16 measurements. Differences between habitat means were significant at the

1 per cent level for 9 measurements and at the 5 per cent for 2 measurements.

The nature of the selective process of bairdi is suggested by the results of Experiment V in which the artificial-grass habitat opposed tree trunks with artificial grass (Table XVI). The values of all 4 measurements were higher in the artificial-grass habitat than in the habitat composed of tree trunks and artificial grass, but significant differences between the habitat means occurred at the 5 per cent level for only 2 measurements, activity-wheel turns and seeds eaten. This result, in comparison with the results of Experiment IV in which the opposing tree trunks were not associated with artificial grass, suggests that bairdi was definitely attracted to artificial grass but that it avoided tree trunks to only a slight extent. The slight tendency to avoid tree trunks may account for the fact that bairdi in nature is not found even in those woodlands that have a grassy ground cover.

In summary, P. m. bairdi in these experiments selected artificial habitats containing objects having a grasslike form. The response to the artificial grass seemed to be mostly positive, but a slight negative response to tree trunks may also have been present.

The experiments described above give a small amount of evidence about the sensory nature of the stimulus received by the mice in making a selection of artificial habitats. In Experiment IV both subspecies selected artificial vegetation corresponding to their natural habitats, even when the reaction room was in darkness. Also, in Experiment VI bairdi made a clear-cut selection under the same condition of darkness. The general inactivity of the mice during the 12-hour period of bright light precludes the possibility that they could have learned the experimental situation and made a selection during that period. Thus, the selective process is able to operate independently of visual stimuli.

In an effort to learn if the stimulus resulting in artificial-habitat selection was a tactile one received through the vibrissae, the mice were tested in Experiment VIII after the vibrissae had been removed. Four individuals of vibrissaeless gracilis selected the tree-trunk habitat in darkness. Differences between habitat means were significant at the 1 per cent level for 3 of the 4 measurements (Table XV). A preference for the artificial grass by vibrissaeless bairdi was also obtained in this experiment. Differences between habitat means were significant at the 1 per cent level for seeds eaten and water consumed, the 2 best measures of habitat selection. For total time and for activity-wheel turns, higher means were obtained in the artificial-grass habitat than in the tree-trunk habitat, but the differences were not statistically significant (Table XVI).

Of the individuals tested in Experiment VIII, 3 gracilis and 4 bairdi had also been tested in previous experiments. It seems unlikely, however, that, if vibrissae are important in habitat selection, previous learning by these individuals could have been almost completely substituted for a definite dependence upon them. Vibrissae are apparently used to some extent by the mice, for I have observed individuals running along the walls of the compartment without bumping into them at the corners. On the other hand, when the mice were excited or frightened, they frequently bumped into objects in their paths. Further, a few bairdi with vibrissae intact gave much the same performance in a small obstacle course as the same number of bairdi with the vibrissae removed.

These results show, I believe, that neither vision nor the tactile organs of the vibrissae are the chief sensory agencies through which the stimuli used in habitat selection are received by the mice. The incidental observations mentioned above do not disagree with this conclusion. Sensations received through the feet, tail, and other parts of the body may be more important in habitat selection than either vision or the sensory function of the vibrissae. These experiments, however, were not designed for a study of sensory stimuli, and the results are to be regarded merely as suggestive.

The responses of males and females to artificial-habitat selection were examined by analysis of variance. A significant sex difference in habitat selection was present in only 1 measurement, that of seeds eaten by gracilis in Experiment IX. When the data for similar experiments were pooled, however, significant differences between sexes were sometimes indicated. Perhaps the differences were not significant in the analyses of single experiments because so few individuals of each sex were involved. As far as these experiments are concerned, it is possible, therefore, that sex differences in artificial-habitat selection may occur, but it seems unlikely that sexual selection of gross differences in habitat would characterize the behavior of these mice in nature.

No consideration has been given to possible seasonal changes in habitat selection inherent in the mice. This was not practical in the present investigation because of limitations of time and equipment. No suggestion was obtained, however, of any change in the habitat preference of the subspecies correlated with the progression of the outdoor seasons.

FACTORS WHICH MAY HAVE INFLUENCED RESULTS OF THE EXPERIMENTS

Factors other than artificial vegetation which may have influenced the responses of the mice in the experiments should be considered. The possibility that the mice may have selected or avoided one compartment or the other, rather than the artificial vegetation therein, must be examined. Such a possible selection or avoidance may have been due to some irrelevant factor connected with the compartment, as, for example, its position. To control these possible effects of position, the artificial habitats were changed from one compartment to the other at least once during each experiment following Experiment III.

TABLE XVII

Statistical Analysis of Habitat-selection Data Divided According to Compartment of the Reaction Room. Values of t and F are for differences between north and south compartments.

Experiment	t Values		F Values			
	Total Time in Compartment		Seeds Eaten in Compartment		Water Consumed in Compartment	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
IV Tree vs. grass	0.72	0.35	16.33**	0.00	1.34	3.20
V Tree + grass vs. grass	0.54	0.88	2.21	6.23*	0.63	13.42**
VI Jungle vs. grass	3.73**	2.06*	14.77*	16.21**	5.06*	2.26
VII Jungle vs. tree: ventilating fan at one end of room	1.74	. . . .	16.98**	. . . .	14.19**	. . . .
VIII Tree vs. grass: mice with vibrissae removed	0.54	2.09*	2.41	6.63*	4.75*	6.18*
IX Jungle vs. tree: ventilating fan in middle of room	1.20	. . . .	0.02	. . . .	5.65*	. . . .
X Tree vs. grass	bairdi x gracilis 0.98		bairdi x gracilis 2.91		bairdi x gracilis 8.47**	

* Value is significant at 5 per cent level.

** Value is significant at 1 per cent level.

To evaluate the effect of position, the data obtained for the measurements of total time, seeds eaten, and water consumed were tabulated by compartment rather than by artificial habitat and were statistically analyzed as already described. In this analysis differences appear between north and south compartments in place of differences between artificial habitats. The F and t values for differences between north and south compartments are set forth in Table XVII. Of the 2 compartments, the one showing the higher value for each experiment and for each measurement is indicated in Table XVIII. From Table XVIII it is seen that, although there is some consistency within an experiment for the compartment with the higher value, there is little consistency in this regard from experiment to experiment.

TABLE XVIII

Summary of Habitat-selection Data Divided According to Compartments of the Reaction Room. The compartment which has the higher of the 2 totals for each measurement is indicated.

Experiment	Total Time in Compartment		Seeds Eaten in Compartment		Water Consumed in Compartment	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
IV Tree vs. grass	north	south	north††	north	north	north
V Tree + grass vs. grass	north	north	north	north†	north	north††
VI Jungle vs. grass	south††	south†	south††	south††	south†	south
VII Jungle vs. tree: ventilating fan at one end of room	south	. . . .	south††	. . . .	south††	. . . .
VIII Tree vs. grass: mice with vibrissae removed	north	south†	north	south†	south†	north†
IX Jungle vs. tree: ventilating fan in middle of room	north	. . . .	north	. . . .	north†	. . . .
X Tree vs. grass	bairdi x gracilis south		bairdi x gracilis south		bairdi x gracilis south††	

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

In comparing Table XVII with the appropriate entry (variation between habitats) in each of Tables I, III, V, VII, IX, XI, and XIII, and with the text, it is noted that the F and t values are generally lower for differences between compartments than for differences between artificial habitats. This is especially true in those experiments where a definite selection for artificial habitat occurred (Experiments IV and VIII for both subspecies, V for gracilis, VI for bairdi, and X for the hybrids). Where no strong selection was manifested by Peromyscus, the F and t values for compartment differences were not so much lower or were somewhat higher than those for differences between artificial habitats. This suggests that, where a combination of artificial habitats did not stimulate selection by the mice, some other less important difference between the compartments received their attention.

Another factor may have complicated the analyses of the data for north and south compartments. The number of mice tested when a given habitat was in one compartment was not always the same as the number tested when that habitat was changed to the other compartment. For example, in an experiment 5 bairdi may have been tested when artificial grass was in the north compartment, but only 3 bairdi when it was in the south compartment. The evidence from the F and t values has indicated that the main difference between compartments was the artificial vegetation. If bairdi selected the artificial grass in the example given above, an analysis of north and south compartments would show favor to the north compartment since more mice were tested when artificial grass was present there and fewer mice when artificial grass was present in the south compartment. A qualitative analysis of the data seems to accord with this belief. Hence, the analysis for north and south compartments may show more difference between compartments than really existed.

The use of the introduction box, previously described, considerably reduced the chance that cues for selection might have been given by the experimenter when he entered the room through 1 compartment to release the mouse. Also, the mouse was free to turn in either direction upon entering the runway apparatus, and thus the first artificial habitat entered would presumably be a matter of chance. Most of the mice remained in the box until long after the experimenter left the room, but occasionally a nervous individual would leave almost instantly.

Preliminary studies revealed that many mice formed a habit of returning to the nest box first occupied during a test. An attempt to break this habit by substituting each day a clean nest box for the one previously used by a particular mouse was not completely successful. Lack of more complete success was apparently occasioned because the introduction box must often have represented the nest box first occupied. The mice first entered the reaction room from the introduction box, and some individuals returned each day to the area between the swinging doors of the runway, which was the closest approach to the introduction box. There is no evidence that nest-box habit influenced those activities of the mice which provided the measures of artificial-habitat selection.

Several procedures were employed to eliminate the possibility that odors left by a mouse influenced the behavior of any mouse tested later in the reaction room. In those experiments in which both subspecies were investigated (except in Experiment VIII), the subspecies were alternated, that is, a test for an individual of one subspecies would be followed by a test for an individual of the other subspecies. By this procedure it is believed that, if a scent pattern should be laid down in some manner by one subspecies, it would be nullified by that of the other subspecies. In the statistical sense this is an attempt to randomize the scent factor. It was occasionally impossible to adhere strictly to this procedure, sometimes because of the death of a mouse in the training cage, and sometimes because of failure of a mouse to enter both habitats during the first night. As another precaution, after the 4-night test period of each individual, the sand on the floor of the 2 compartments was mixed and smoothed with a brush. Also, after each mouse was tested, the activity wheels, nest boxes, food dishes, and water tubes and racks were washed in water. Between experiments the sand was sifted to remove mouse droppings and other debris. It may be doubted, therefore, that the habitat selection of a mouse was seriously influenced by the scent left by mice previously tested in the reaction room.

The reaction room in which the experiments were conducted is not soundproof. At one end of the room the ventilating fan made a continuous buzz during most of the experiments, while near the other end of the room the reducing gears of the recording apparatus could be heard through the wall. These and less regular sounds were randomized by exchanging the artificial habitats from compartment to compartment during the course of each experiment.

The temperature varied somewhat in different parts of the reaction room, partly because in winter warm air entered one end of the room and became cooled as it passed toward the outlet at the other end. Radiation of heat from the walls of the room also affected the temperature. The reaction room is situated in a corner of the building; 2 walls of the south compartment and 1 wall of the north compartment are outside walls. Less heat radiates from the outside walls; hence the south compartment was somewhat cooler than the north compartment. During warm periods of the year the air temperature near the floor varied about 2^o F. from place to place in the room, but during cold weather it varied as much as 8^o F. The effect of this temperature variation was randomized by reversal of the artificial habitats during each experiment.

Relative humidity in the reaction room was low during the winter owing to artificial heating of the building. It must have differed from place to place in the room at those times when a gradient of air temperature occurred. The possible differences between compartments in air humidity were randomized by changing the artificial habitats.

Air currents in the room are believed to have had no effect on the reactions of the mice. None of the air currents was of sufficient strength to cause any perceptible movement of the artificial grass.

The effect of light intensity on habitat selection has already been described in Experiments II and III. The preference for artificial grass and for tree trunks by bairdi and by gracilis, respectively, appeared to be less definite when the intensity of the night light was reduced in the unpreferred habitat than when it was reduced in the preferred habitat. Light intensity was controlled in all the experiments following Experiment III by equalizing the light intensities on the floors of the 2 compartments (Experiment V) or by using no lights during the 12-hour night period.

RELIABILITY AND VARIABILITY IN SELECTION OF ARTIFICIAL HABITATS

The experiments described demonstrate that the 2 deermouse subspecies, bairdi and gracilis, under controlled laboratory conditions usually selected different types of artificial habitat. P. m. bairdi, with very few exceptions, selected the artificial-grass habitat in all experiments, as indicated by each of the 4 measures of habitat selection. Similarly, gracilis, with few exceptions among the 4 measures, selected the tree-trunk habitat in those experiments in which tree trunks were contrasted with the artificial-grass habitat. It has been demonstrated further that the most important difference between the 2 compartments to which the mice responded was the artificial vegetation. It may be concluded, therefore, that the experimental technique was adequate to measure habitat selection. Similarly, the consistency with which the activities of eating, drinking, and, to a less extent, running in the activity wheel were pursued more by a particular subspecies in one type of habitat than in the other, together with general activity as measured by total time, indicates that these are valid measures of habitat selection.

In spite of the evidence that bairdi preferred the artificial grass and that gracilis preferred the tree trunks, neither form entirely avoided the opposite type of habitat in these experiments. A complete avoidance would not be expected in view of the small area of the reaction room as compared with the area of the individual home range of either race in nature. The average size of the home range of adult bairdi in nature, as determined by Blair (1940), is 0.63 acre for males and 0.51 acre for females, but Howard (1949) presented evidence for a home range of several acres. The size of the average home range of adult male gracilis is 2.31 acres and of adult female gracilis is 1.39 acres (Blair, 1942). The small area (.004 acre) of the reaction room would be expected to affect artificial-habitat selection by reducing its strength, but this did not occur to such an extent that selection could not be demonstrated. On the other hand, the areas of the 2 compartments were so small that a mouse could investigate all parts of each of them during the first night of testing and could then proceed to select between the 2 artificial habitats which they contained.

The analyses of variance of turns of the activity wheel, number of seeds eaten, and amount of water consumed demonstrate that, of the 6 sources of variation for each of these measures of habitat selection, differences between habitats and between habitat-individual interaction are most often statistically significant. Also, these 2 sources of variation show, in most cases, high F values. Usually the F values for habitat differences are higher than those for habitat-individual interactions. Thus, the sources of significant variation in the analyses of variance are differences between habitats and between habitat-individual interaction.

A significant interaction between habitat and individuals means that in an experiment different individuals react to habitat differences with significantly different degrees of strength, even though as a group all of the individuals in that experiment reacted significantly to 1 type of artificial habitat. It should be emphasized that in the statistical computations a significant difference in reaction to habitats is in no way affected by a significant individual-habitat interaction.

Variation among individuals is less often significant for each of the 3 measures of habitat selection in all the experiments than is variation between habitats or habitat-individual interaction. Of the 3 measures of habitat selection in which individuals show significant variation, wheel activity supplies almost two-thirds of the occurrences. The few instances of significance among the remaining sources of variation, that is, variation among days of a test, variation in habitat-day interaction, and variation in individual-day interaction, occurred with 1 exception (habitat-day interaction for water in Experiment X) for the measure of activity-wheel turns. The fact that these several sources of variation show statistical significance most often in turns of the activity wheel is due to the great variation in the use of the wheel by different mice. The studies by Dice and Hoslett (1950) of activity-wheel records of several laboratory stocks of Peromyscus demonstrate great variability among individuals.

Thus the analyses of variance of seeds eaten and of water consumed reveal that no great amount of statistically significant variation, other than variation between habitats and variation in habitat-individual interaction, exists in these experiments. The variation in turns of the activity wheel has been explained. Variation between habitats is characteristically more significant (higher F values) than is variation in habitat-individual interaction. The differential response of a subspecies to the artificial habitats is the significant variable in the experiments, and the measurement of this response is the object of this investigation.

The relative effectiveness of the several methods for measuring habitat selection may be estimated by the frequency with which the measurements reveal a statistically significant difference in artificial-habitat selection by the mice. If each experiment and each race and the hybrids of Peromyscus are considered separately, 13 occurrences of a statistically significant habitat selection were possible for each measure. A statistically significant habitat selection, as measured by the number of seeds eaten, occurred in 11 of the 13 possibilities; as measured by the amount of water consumed, in 9 of the 13 possibilities; as measured by the total time in each habitat, in 7 of the 13 possibilities; and as measured by the number of turns of the activity wheels, in 7 of the 13 possibilities. Accordingly, the number of seeds eaten and the amount of water drunk appear to be the best measures of artificial-habitat selection by the mice. Total time is a better measure than activity-wheel turns, since the latter, as explained above, showed considerable variability among individuals. Activity-wheel turns could have been eliminated as a measure of artificial-habitat selection.

An attempt was always made to use different mice in the experiments (except in Experiment VIII), but because of lack of breeding during winter in the gracilis stock not many new individuals of this subspecies were available for the later experiments. The purpose in avoiding repetition in the individuals tested was to prevent modification and change of artificial-habitat selection by the mice due to learning and remembering. The reactions to artificial habitats of 8 out of 9 mice that were tested more than once in different experiments can be compared. Four of these mice showed consistent selection of a particular habitat type, 2 showed inconsistent selection, and 2 reversed the habitat type selected. Also, 3 individuals were by error tested twice in Experiment V. One was consistent in habitat selection, 1 showed partial reversal, and 1 showed complete reversal in the habitat chosen. No corrections or eliminations were made in the statistical analyses for the individuals that were tested more than once. These few data do not give evidence that change in artificial-habitat selection by a mouse tested in different 4-day periods is due to learning and remembering. They do indicate that it is wise to avoid repeating tests of the same mouse in the same or in similar experiments.

It seems reasonable that learning would weaken artificial-habitat selection by increasing the variability of the response. Such an effect would have to occur in most cases within the 4-day test period of each mouse, and the statistical evidence indicates that variation in the response of the mice among days of the test period was, in general, due to chance. Furthermore, the results of most of the experiments show that selection did occur in spite of any learning that might have weakened it.

The laboratory cages in which the mice were born and lived may also have conditioned them in a way to modify their preference for a particular artificial habitat. If this happened, and it is not possible to determine whether or not it did, it would probably have weakened the effect of their selection.

There is no evidence that learning and habit formation reinforced instinctive habitat selection by the mice in the experiments. Undoubtedly, habit formation entered into the reaction of the mice to artificial habitats, and it is possible that it may have reduced the sharpness of the selection which occurred. The probability that learning occurred does not affect the conclusions with reference to artificial-habitat selection by Peromyscus in these experiments.

FACTORS SELECTED IN THE HABITAT

A number of ecologists have discussed the problem of habitat selection by animals (Shelford, 1911; Grinnell, 1917; Dice, 1931b; and others). Elton (1927: 39-41) treated the subject rather fully. He believed that most animals are limited in their distribution by their habits and reactions. Their reactions presumably are suited to their particular physiological requirements and to their breeding habits. The stimuli which cause this distributional limitation, presumably to the optimum conditions for their life, may not themselves be directly harmful to the animal; they probably are more in the nature of signs or cues, warning the animal that it is approaching less suitable conditions for life. Thus, the immediate causes of the limitation in distribution may often be found in the psychological reactions of the animal.

Factors Previously Suggested by Authors

Among the factors that have been previously suggested by various authors as controlling the habitat distribution of animals, meteorological factors, light intensity, food and water, nesting sites, and interspecific dominance merit particular attention.

Meteorological Factors. — The effect of the evaporating power of the air on the reactions of Peromyscus leucopus noveboracensis, a woodland and brush-inhabiting species, was studied by Chenoweth (1917). In his experiments the mice were free to choose between different evaporating powers of air in a gradient apparatus. He concluded that evaporation rate, whether produced by movement, dryness, or temperature of the air, is probably the most important factor in determining the habitat distribution of this species.

The quantity of water and food used by Peromyscus l. noveboracensis and P. maniculatus bairdi under different conditions of air temperature and humidity was studied by Dice (1922). His experiments did not show sufficient differences between the 2 species of Peromyscus in their requirements for food, water, temperature, and air humidity to explain their habitat differences. Thus, he did not substantiate Chenoweth's conclusion in regard to habitat selection by P. l. noveboracensis.

The effect of climatic conditions on these same 2 species of Peromyscus was studied by Johnson (1926). Principally by comparison of climatic records obtained in both field and woodland habitats, he concluded that climatic factors do not explain the restriction of the 2 species to their respective habitats. He believed that their habitat distribution depends upon the whole biotic association type, rather than on any single factor of the environment.

Light Intensity. — Certain experimental evidence indicates the importance of light intensity to nocturnal mice. Moody (1929) showed that P. m. gracilis can distinguish from darkness a light intensity of 1.13×10^{-6} candle power per square cm. It has been shown experimentally that the activity of deermice is related to the intensity of light. In very dim light or darkness they move about freely. As the light intensity increases, the activity of the deermice decreases until a threshold is reached at which they do not leave their nest boxes (Blair, 1943).

Kalabukhov (1938) studied the selection of several intensities of light by closely related species of Apodemus and Citellus and considered the results in relation to habitat restriction. He found that in a gradient apparatus Apodemus sylvaticus avoided bright illumination to a considerably greater degree than did A. flavicollis. In nature the former species seems to be the more strictly nocturnal of the two. Kalabukhov believed that A. sylvaticus lives in brushy and open habitats more commonly than A. flavicollis because the more strictly nocturnal habits of the former give it a greater degree of protection from predators. He found no marked difference between the reactions of 2 species of Citellus to light intensity.

The experiments discussed above indicate that light intensity has an influence of some importance on the activities of nocturnal mice. It is possible that light intensity has also some influence on habitat selection by mice, but this factor was not measured in the present investigation.

Food and Water. — The fact that the food and water required by Peromyscus m. bairdi and P. l. noveboracensis probably do not constitute an important factor in limiting their habitat distribution (Dice, 1922) has already been discussed. This conclusion, as to food, has been further substantiated by Cogshall (1928), who in the laboratory offered a choice of many different foods to the forms of Peromyscus mentioned above and also to P. m. gracilis and to P. m. sonoriensis.

Nesting Sites. — The possibility that Peromyscus l. noveboracensis is limited to woodlands and that P. m. bairdi is limited to open habitats because of a nesting site preference has been considered by Johnson (1926). He concluded from a few observations that nesting sites do not explain the habitat restrictions of these 2 species. On the other hand, Nicholson (1941) believed that P. l. noveboracensis showed a definite preference for artificial nest boxes placed above the ground. I have seen individuals of P. m. gracilis, when released from live traps, run into hollow logs, holes at the bases of stumps and trees, holes in tree trunks several feet above the ground, and occasionally into holes in the ground. My few observations suggest that gracilis usually uses refuges associated with tree trunks and stumps.

It is possible that the preference of a given race of Peromyscus for a particular type of nesting site may contribute to its restriction to a particular type of habitat. Much more critical study is required to ascertain the role of nesting site in habitat restriction of Peromyscus. In the experiments here described nesting site could not have been a deciding factor.

Interspecific Dominance. — There is no evidence that antagonism between P. m. bairdi and P. l. noveboracensis is an important factor in preventing one species from invading the habitat of the other (Dice, 1922). Observations have shown that these 2 species may in nature form mixed aggregations (Nicholson, 1941; Howard, 1949). Close association apparently may occur between 2 individuals of different species, for almost half of the double captures made with single-catch live traps included mice of 2 species (Evans and Holdenried, 1943). These writers remarked on the infrequency of fighting between 2 species of Peromyscus in the same live trap as compared with double captures of Peromyscus with Perognathus. In the Laboratory of Vertebrate Biology, groups of 3 individuals each of gracilis and bairdi commonly associated even when they had opportunity to live in separate cages (unpublished data of the author). These data accord with Dice's conclusion of a lack of interspecific antagonism and extend it to the 2 subspecies tested in the present study.

Other Factors. — Other factors also may influence the habitat preferences of Peromyscus, but none has been adequately treated in the literature from this viewpoint. For example, soil texture is important in the distribution of the kangaroo rat (Hardy, 1945:101). It is doubtful if soil type can be a factor which directly restricts bairdi to open habitats and gracilis to wooded or brushy ones. In its extension of range, bairdi has come to inhabit regions where soil was originally developed under woodland and has since been modified by agriculture and resulting soil erosion. Furthermore, bairdi usually excavates simple and shallow burrows and often uses abandoned burrows made by other species of animals (Howard, 1949). Also, my observations indicate that gracilis uses refuges associated with stumps, logs, or hollows in trees more frequently than it uses unprotected burrows in the soil.

Meteorological factors, food and water, nesting sites, intraspecific dominance, and soil type do not appear, separately, to be factors of importance in limiting the several kinds of Peromyscus to their particular habitats. Intensity of light is of importance in regulating the activity of nocturnal mice, but there is no good evidence that it is a factor which limits them to different habitats.

Limiting Factors Suggested by the Present Study

In the present study the reactions of 2 subspecies of Peromyscus maniculatus to contrasting types of simplified artificial habitats have been measured by experimental methods. The simplified habitat types were designed to simulate the characteristic vegetation of certain natural habitats: forest, grassland, and brushland.

It has been demonstrated that the artificial habitats in the experiments presented the main differences used by the mice in choosing between the 2 compartments of the reaction room. The artificial habitats were composed of objects made to resemble natural vegetation. Although the sections of tree trunks were less artificial than the grass made from Manila folders, they were not living. They were limited in height, and the environment surrounding them (with the exception of Experiment V) was devoid of cover, such as is provided by herbaceous plants in natural forest communities. Reduced to simple terms, habitat selection by gracilis and by bairdi seems to be based to at least a considerable extent on an attraction toward certain objects characteristic of their natural habitats. Thus, gracilis is attracted by tree trunks, while bairdi is attracted by grasslike objects.

The precise characteristics of the objects to which bairdi and gracilis responded were not ascertained in these experiments. P. m. bairdi may have responded to the shape of the grasslike objects, or possibly it responded to the close spacing of the artificial-grass blades, which may have given it a sense of security. P. m. gracilis, in turn, may have responded to the shape of tree trunks or trees, or it may have responded to objects which permitted it to climb upon them (Horner, 1948). Rigidity, as opposed to the flexibility of grass blades, might be an important characteristic of objects selected because of the arboreal adaptation of gracilis. The hypothesis, however, that habitat selection by gracilis is based on its arboreal adaptation is not supported by the experiments using jungle as one of the artificial habitats. The jungle supplied rigid objects suitable for use in climbing which were not similar to tree trunks. Yet gracilis showed no preference for jungle when it was given a choice between jungle and artificial grass (Experiment VI). On the other hand, no preference was shown for either jungle or tree trunks when they were presented for selection (Experiments VII and IX), and this result would be expected if habitat selection were based on a semiarboreal adaptation. Hence, the experiments involving jungle as one of the artificial habitats present conflicting evidence for the importance of semiarboreal adaptation in habitat selection by gracilis.

It is difficult to believe that the vegetation itself could ever be a direct cause of the death of an individual mammal that is not in its normal habitat. Evidence that a species of mammal may exist and apparently thrive in a habitat that it would not select if given a choice has been presented by Dice (1925). Normally the meadow vole, Microtus p. pennsylvanicus, lives in grassy areas. On Marion Island, Grand Traverse County, Michigan, however, this species was discovered living in fairly dense hardwood forest. It occurred there with other species of small mammals which are normally found in that type of habitat. Since most of the island was covered with forest and only small areas of open land were present, Microtus here had little choice of habitat.

It appears likely, therefore, that objects in the environments of the several forms of Peromyscus present cues by which these mice select their preferred habitats, but that under certain circumstances some animals can exist in habitats which they would not normally select.

Evidence that animals use cues in their selection of habitats has been presented by Lack (1933). He studied the birds that occurred in pine plantations of different ages and heights in England. By comparing the habitats in which particular species lived, he concluded that the cue for habitat selection by certain species of birds was apparently the height of the vegetation rather than its type. Other species seemed to react to preferred types of singing perches or nesting sites. Such factors Lack referred to as psychological factors.

The results of my experiments suggest that in nature objects, such as the type of plant, may be the cues by which the various races of Peromyscus select their habitats. To what extent this may be true of other kinds of animals is unknown.

It seems likely that a species is adapted to the objects which it uses as cues in selecting its habitat. For instance, the long-tailed forest-inhabiting forms of Peromyscus have been shown by Horner (1948) to possess a definite semiarboreal adaptation in comparison with the short-tailed forms which inhabit open fields. One of these long-tailed forms, P. m. gracilis, has been shown in this paper to select tree trunks in preference to artificial grass, which are objects to which it is adapted in its natural environment. Peromyscus leucopus noveboracensis, another long-tailed woodland form, likewise has shown in its use of artificial nest boxes a preference for nesting sites situated above the ground (Nicholson, 1941).

HEREDITY OF HABITAT SELECTION

Most animals tested in the first 3 experiments were field caught. Because it was not known at the beginning of the study whether habitat selection is due to conditioning or to instinct, it was thought that individuals previously conditioned in nature would react more strongly to the artificial habitats than laboratory-bred mice. A constant supply of field-caught Peromyscus m. gracilis was impossible to obtain, however, and only laboratory-bred mice of both subspecies were tested in Experiment IV and in subsequent experiments.

Because the laboratory-bred animals were kept in standard laboratory cages, they had had no previous experience either with natural or with artificial habitats of the type used in these experiments. In view of their lack of previous experience, it is concluded that the habitat preferences expressed in these experiments must have resulted from instinctive behavior.

Further information on the heredity of artificial-habitat selection was obtained in Experiment X by testing F_1 hybrids produced by matings between individuals of female bairdi and male gracilis. The 7 hybrid individuals tested exhibited a preference for the artificial-grass habitat which was contrasted with the tree trunks. This preference was significant at the 5 per cent level for one measurement and at the 1 per cent level for 3 measurements of habitat selection (Table XIX). Thus, the genetic mechanism responsible for selection of artificial grass is at least partly dominant over that responsible for the selection of tree trunks. The

TABLE XIX

Summary of Selection Between Artificial-grass and Tree-trunk Habitats by Peromyscus m. bairdi x P. m. gracilis F_1 Hybrids in Experiment X.

Light Intensity (in f.c.)	Habitat with the Higher Mean			
	Total Time in Habitat	Activity-Wheel Turns	Seeds Eaten	Water Consumed
Dark	grass††	grass†	grass††	grass††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

F values for the several measurements of habitat selection by the hybrids were, in general, lower than those for the parental subspecies. Also, there was a significant variation among the hybrid individuals for the measures of wheel turns, seeds eaten, and water consumed. This indicates a greater degree of variability in habitat selection by the hybrids than by either of the parents, bairdi or gracilis.

It is probably true that the first instinctive act of an animal may be reinforced by learning and conditioning, but this in no way invalidates the conclusion that artificial-habitat selection is based on instinctive behavior. There is no evidence in the experiments to show that instinctive acts of an animal may be reinforced in this manner. Such a reinforcement would have to appear during the 4-day test given each mouse. Each mouse varied from day to day in the proportion of its reactions in each artificial habitat, and each mouse differed in this respect from every other mouse. There was no consistent trend among the mice toward a more definite habitat selection as the 4-day test periods progressed.

Habitat selection in nature, however, is probably not entirely an instinctive process. These experiments deal only with artificial habitats that differ widely from each other, such as forest contrasted with open fields. Selection of more local conditions within such habitats might well be modified by experience as suggested by Miller (1942:34).

The instinctive selection of objects in the habitat may be assumed, in accordance with the modern theory of evolutionary processes, to have developed in animals in response to natural selection. The evolutionary importance and significance of habitat selection have been discussed by Elton (1930), Lack (1933, 1940), Miller (1942), and Thorpe (1945).

SUMMARY

In nature mice of the subspecies Peromyscus maniculatus bairdi are closely restricted to open-field habitats, while the subspecies P. m. gracilis lives most commonly in hardwood forests and to a lesser extent in brushy habitats. To ascertain the factors responsible for these habitat preferences, selection for artificial habitats by bairdi and gracilis was measured under controlled experimental conditions.

The artificial habitats presented to the 2 races of Peromyscus were tree trunks, artificial grass, and jungle, the last composed of a latticework of sticks. Selection by individual mice between 2 of these artificial habitats was made possible in each of 10 experiments by placing a different artificial habitat in each of 2 compartments of a reaction room. The habitat preference of each mouse was measured for 4 consecutive nights by recording (1) the number of sunflower seeds eaten, (2) the amount of water drunk, (3) the number of turns made in activity wheels, and (4) the total time spent in each of the 2 artificial habitats. The data obtained from these measurements were treated statistically.

In these experiments, bairdi is shown to have selected the artificial-grass habitat in preference to either the tree-trunk or the jungle habitat. The differences in this preference were significant at the 5 per cent or at the 1 per cent level for 9 out of 12 measurements involving 3 experiments. The tree-trunk habitat was selected by gracilis in those experiments in which this habitat was contrasted with the artificial-grass habitat. The differences in preference between these 2 artificial habitats were also significant at the 5 per cent or at the 1 per cent level for 9 out of 12 measurements involving 3 experiments.

The selection of these 2 artificial habitats by the 2 races of Peromyscus seems to be a selection for particular kinds of objects in the environment. These objects probably act as cues by which the mice recognize the environment most suitable to them.

Selection of the artificial-grass habitat by bairdi and of the tree-trunk habitat by gracilis was successfully made in darkness both by normal mice and by mice from which the vibrissae had been removed. These results indicate that for its habitat selection Peromyscus is independent both of sight and of the tactile sense mediated through the vibrissae.

Laboratory-bred Peromyscus which had had no previous experience either with natural habitats or with artificial habitats simulating natural ones were tested in some of the experiments.

Each subspecies exhibited a preference for the type of habitat which it normally inhabited in nature. It may be concluded, therefore, that habitat selection by Peromyscus is basically genetic in nature. The trait of selection for the artificial-grass habitat is, to some extent, dominant in heredity over the trait of selection for the tree-trunk habitat. This is demonstrated by the preference of F_1 bairdi x gracilis hybrids for the artificial-grass habitat over the tree-trunk habitat. The preference was statistically significant in all 4 measurements of habitat selection.

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PLATE I

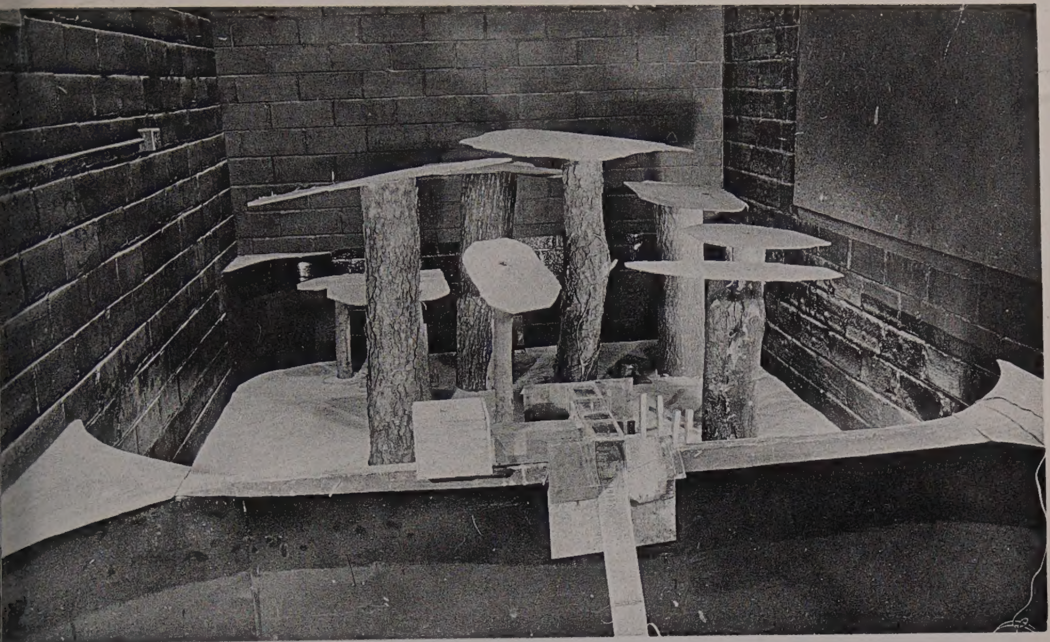

Fig. 1. The artificial tree-trunk habitat in a compartment of the reaction room. In the foreground is he partition which separates the tree-trunk compartment from the artificial-grass compartment. The runway across this partition, together with part of the recording apparatus, is in the middle foreground.

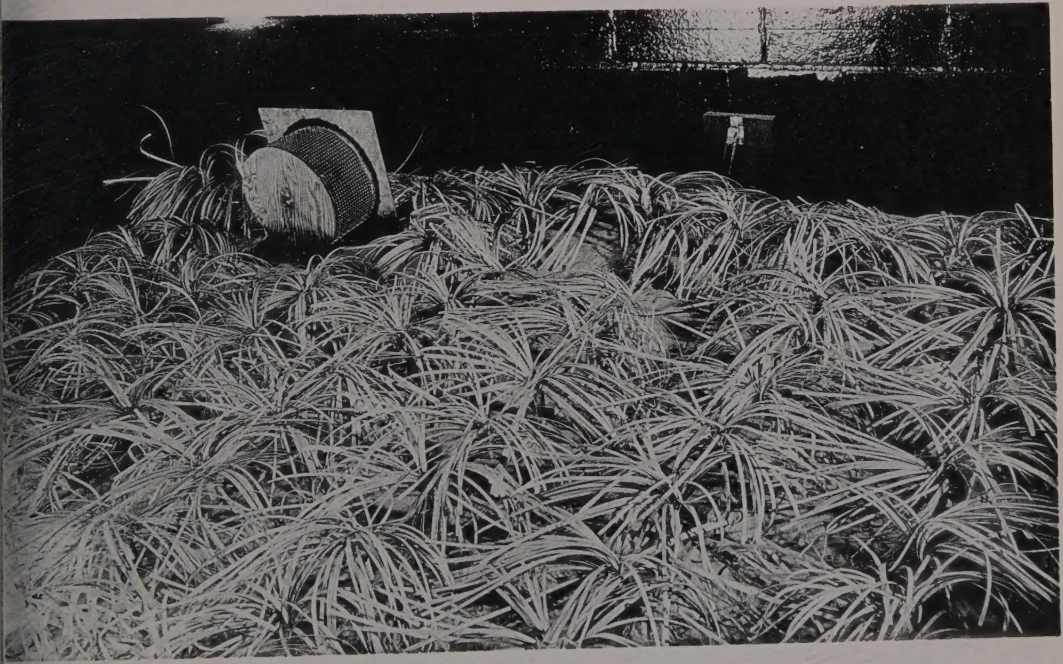

Fig. 2. Part of the artificial-grass habitat in a compartment of the reaction room. The activity wheel is in the left background and the water tube and rack in the center background.

PLATE II

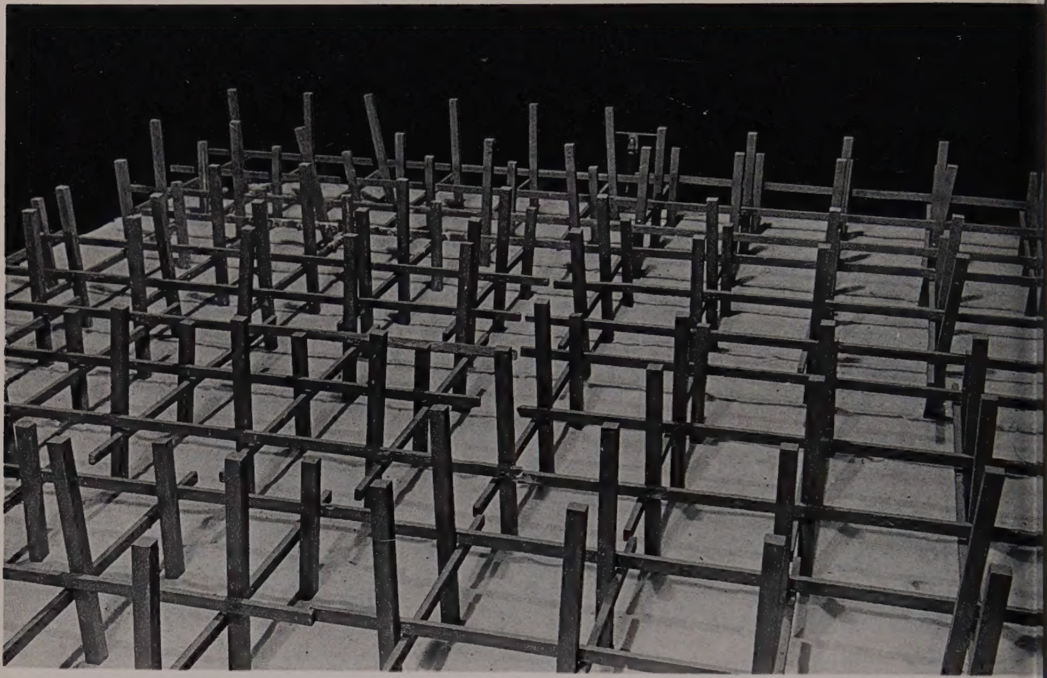

Fig. 1. The artificial jungle habitat.

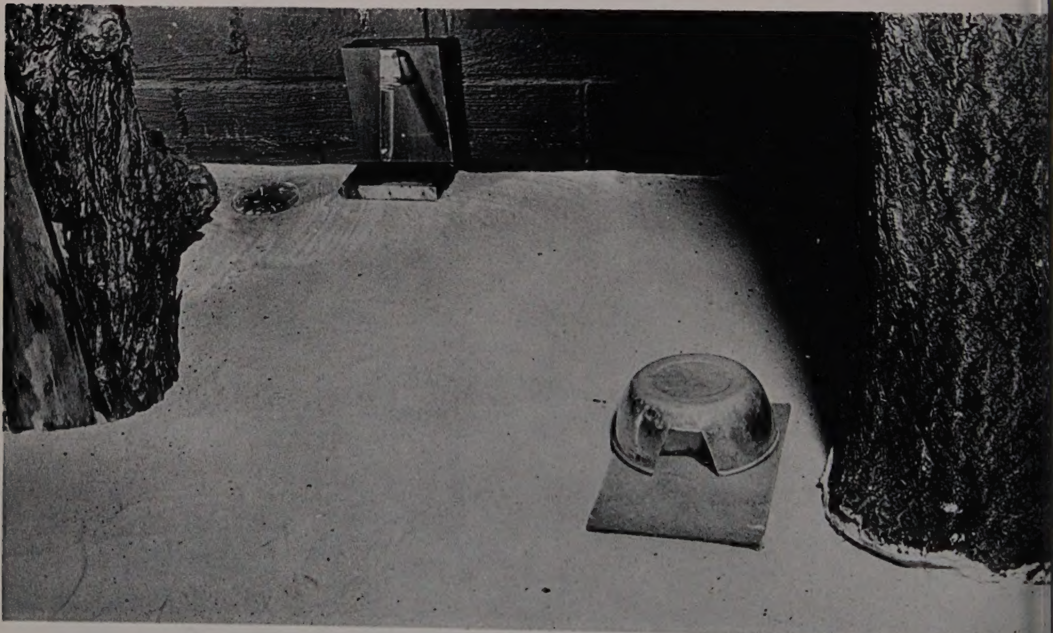

Fig. 2. An experimental compartment. Left to right: tree trunk, food dish, water tube and rack, ne
box, and tree trunk.